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Anatomy of the prosauropod dinosaur *Blikanasaurus cromptoni* (Upper Triassic, South Africa), with notes on the other tetrapods from the lower Elliot Formation

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With 8 figures

Kurzfassung: Der Holotyp (ein unvollständig erhaltenes Hinterbein) des prosauropoden Dinosauriers *Blikanasaurus cromptoni* GALTON & VAN HEERDEN 1985 wird aus der unteren Elliot Formation (Red Beds, Karn, Obertrias) beschrieben. *Blikanasaurus* bildet, zusammen mit den sympatrischen Gattungen *Euskelosaurus* und *Melanorosaurus*, das älteste Vorkommen der Prosauropoda (zumindest was artikulierte Reste betrifft). Die prosauropode Familie Blikanasauridae ist durch ein extrem plumpes Hinterbein – insbesondere im Metatarsus – charakterisiert. *Blikanasaurus* kann als ein schwergewichtiger quadrupeder Saurischier angesehen werden, steht aber wahrscheinlich nicht in der Vorfahrenlinie zu den Sauropoden. Es wird ein Überblick über die übrigen Tetrapoden der unteren Elliot Formation mit besonderer Berücksichtigung des carnivoren Dinosaurier *Aliwalia rex* gegeben.

Abstract: The holotype of the prosauropod dinosaur *Blikanasaurus cromptoni* GALTON & VAN HEERDEN 1985, a partial hindlimb, is described from the lower Elliot Formation (Red Beds; Carnian, Upper Triassic) of the Eastern Cape, South Africa. *Blikanosaurus*, along with the sympatric *Euskelosaurus* and *Melanorosaurus*, probably represent the oldest record of the Prosauropoda (certainly so for articulated remains). The prosauropod family Blikanasauridae is characterized by a hindlimb that is extremely stocky, especially the metatarsus. *Blikanasaurus* was an early heavily-built, quadrupedal saurischian, but it was probably not the ancestor for the Sauropoda. The other tetrapods of the lower Elliot Formation are reviewed with particular emphasis on the carnivorous dinosaur *Aliwalia rex*.

Introduction

The 'Blikana dinosaur' was found in January 1962 at an altitude of approximately 1.370 m, at a locality ±1.6 km northeast of the trading store at Blikana, in the Herschel district of the Eastern Cape (from a region formerly known as Transkei), South Africa. It was found by Dr. CHRIS GOW, a member of the British-South African Museum Expedition to the Herschel area and Lesotho, at the base of the lower Elliot Formation (Upper Triassic) in the so-called 'Passage Beds' ("for the beds which are lithologically transitional between the typical Molteno Beds below and the typical Red Beds above", CHARIG et al. 1965: 200). The specimen (SAM K403) consists of the left lower hindlimb of a prosauropod dinosaur which is remarkable for the stockiness of its elements.

"The specimen was prepared by immersion in 12% acetic acid after all exposed bone surfaces had been coated with perspex dissolved in chloroform. The period of immersion was twelve hours, followed by washing in water for twice the immersion period" (CROMPTON & WAPENAAR, unpublished). In some places the bone surface was weathered prior to fossilization, which made it most difficult to separate the matrix from the bone, but nevertheless the contours of the different elements can be readily discerned. The measurements were taken with due consideration for unremoved matrix.

In an unpublished description by A. W. CROMPTON & M. L. WAPENAAR, the specimen was tentatively referred to the prosauropod dinosaur *Melanorosaurus,* and this was followed by EWER (1965: 430). CHARIG et al. (1965) briefly described but did not illustrate the 'Blikana dinosaur' as probably representing a new but unnamed family of prosauropod dinosaurs, and this account was summarized by STEEL (1970). RAATH (1972: fig. 10a) reproduced a figure (Fig. 1F), that was provided by A.W. CROMPTON, of the proximal ends of the articulated metatarsals of the 'Blikana melanorosaurid'.

The family Melanorosauridae VON HUENE 1929 is based on the partial skeleton of *Melanorosaurus readi* HAUGHTON 1924 from the lower Elliot Formation of the Karoo basin, South Africa. VAN HEERDEN (1979) redescribed the holotype of this taxon that he regarded as a junior synonym of the sympatric plateosaurid *Euskelosaurus browni* HUXLEY 1866, the common prosauropod from these beds (VAN HEERDEN 1979; KITCHING & RAATH 1984). The Melanorosauridae were discussed by GALTON

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(1985a, 1992). The only well known melanorosaurid is *Riojasaurus incertus* (Fig. 1H-M; Upper Triassic, Norian, Argentina), the hindlimb and ankle region of which were described by BONAPARTE (1972) and NOVAS (1989), respectively. New and more complete material of *Melanorosaurus readi* was described from the lower Elliot Formation of Eastern Cape Province by VAN HEERDEN & GALTON (1997). SAM K403 was briefly described and made the holotype of *Blikanasaurus cromptoni* GALTON & VAN HEERDEN 1985 that was assigned to its own family, the Blikanasauridae GALTON & VAN HEERDEN 1985. The purpose of this paper is to provide a well illustrated description of the holotype of *Blikanasaurus cromptoni*, to consider the relationships of *Blikanasaurus*, and to discuss the associated tetrapod fauna of the lower Elliot Formation.

Abbreviations: BMNH = The Natural History Museum, London, England; GPIT = Institut für Geologie und Paläontologie der Universität Tübingen, Germany; NMW = Naturhistorisches Museum, Wien, Austria; PVL = Colección Paleontología Vertebrados, Instituto 'Miguel Lillo', Tucumán, Argentina; SAM = South African Museum, Cape Town. – A = astragalus; a = anterior intercondylar groove; af = antorbital fenestra; ap = ascending process; as = surface for astragalus; av = alveolus; C = calcaneum; c = cnemial crest; ca = surface for calcaneum; ct = calcaneal tuber; D = distal tarsal; d = lateroventral depression; dp = dorsal process; F = fibula; f = fourth trochanter; ff = facet for fibula; g = greater trochanter; h = head; i = inner (medial) condyle; l = lesser trochanter; Mx = maxilla; o = outer (lateral) condyle; p = posteroventral projection; Pm = premaxilla; pp = posterior process; r = replacement tooth; rt = root of functional tooth; s = inter-dental septum; T = tibia; t = surface for tibia; v = ventromedial projection; 1-3 = metatarsals 1-3.

Systematic Paleontology

Order Saurischia SEELEY 1888
Suborder Sauropodomorpha VON HUENE 1932
Infra-order Prosauropoda VON HUENE 1920
Family Blikanasauridae
GALTON & VAN HEERDEN 1985
Genus *Blikanasaurus* GALTON & VAN HEERDEN 1985

Blikanasaurus cromptoni
GALTON & VAN HEERDEN 1985
Figs. 1A-G, 2-6

Holotype: Left epipodials, tarsus and pes with two or three phalanges missing (SAM K403).

Locality and Horizon: from 1.6 km northeast of Blikana Trading Store, Herschel district, Eastern Cape Province, South Africa, at an altitude of 1.370 m, in the lowermost part of the lower Elliot Formation, Stormberg Group, Karoo Supergroup (Upper Triassic, Carnian, ?lower Carnian GAUFFRE 1993a).

Diagnosis: Tibia with maximum proximal width 0.48 of maximum length, long axes of proximal and distal ends at 60°, distally posterior process relatively deep and robust. Distal end of fibula with a large oval, ventromedially directed articular surface. Astragalus with relatively high, prominent ascending process. Calcaneum small. Metatarsal I short but very robust; metatarsals II, III and IV subequal in length, III being the longest; ratio of maximum proximal width to maximum length for metatarsals I to V is 0.91, 0.72, 0.53, 0.53, 0.74.

Description and comparisons:

Tibia (Figs. 1A, B, D, E, 2N-Q, 3A, 5D)

The tibia has a deep excavation (probably pathological) that runs posteriorly on the proximal part of the head (Fig. 2O). The strongly developed curvature of the posterior edge is probably also pathological. Compared with those of melanorosaurids and plateosaurids (Fig. 1H, I, N), the tibia of *Blikanasaurus* is far more robust. The long axis of the proximal head forms an angle of about 60° with the long axis of the distal end. This is closest to the condition found in the Melanorosauridae, where the angle is 50-55°; in other prosauropods it is usually less than 50°. The shaft of the tibia is triangular in cross-section, the anterior apex forming the cnemial crest on the proximal third of the tibial length. The minimum thickness of the shaft, measured approximately two-thirds down its length, is 71 x 61 mm. In melanorosaurids the cnemial crest is more prominent and occupies almost two-thirds of the length of the tibia. The distal part of the shaft is also triangular in cross-section, but here the apex is directed posteriorly. The distal end of the tibia has the same configuration found in the melanorosaurids and other prosauropods, but the posterior (or descending) process is relatively deep and robust.

Fibula (Figs. 1D, 5A-C)

The fibula lacks the proximal end. At the break the bone is more or less an isosceles triangle in cross-section with the small angle (±30°) directed posteromedially. The distal half of the shaft is subcircular in cross-section. The distal end is slightly expanded medially and the suboval articular surface has two surfaces that meet at an obtuse angle: a larger, more proximal surface that faces anteromedially and ventrally for the astragalus and a smaller, ventrally facing surface for the calcaneum (Figs. 1D cf.1E, 5B, C).

Astragalus (Figs. 1C-E, G, 3, 4A-D, 5D, E)

In dorsal or ventral views (Fig. 4B, D), the astragalus is markedly broader medially (85 mm) than laterally (59 mm). Measured laterally through the robust ascending process (Fig. 4A), the total height is 70 mm and from here it slopes gently downwards medially. The minimum thickness of the bone is toward the medial side where it measures 40 mm. The ascending process itself is approximately 32 mm high, 38 mm broad sagittally and 40 mm transversely. Posterior to the ascending process there is a shallow groove to receive the posterior (or descending) process of the tibia, so that in life the tibia and astragalus interlocked to a considerable extent (Fig. 5D) and movement between the two elements would have been minimal, partly because of the groove and partly because of the high ascending and posterior processes. The ventral

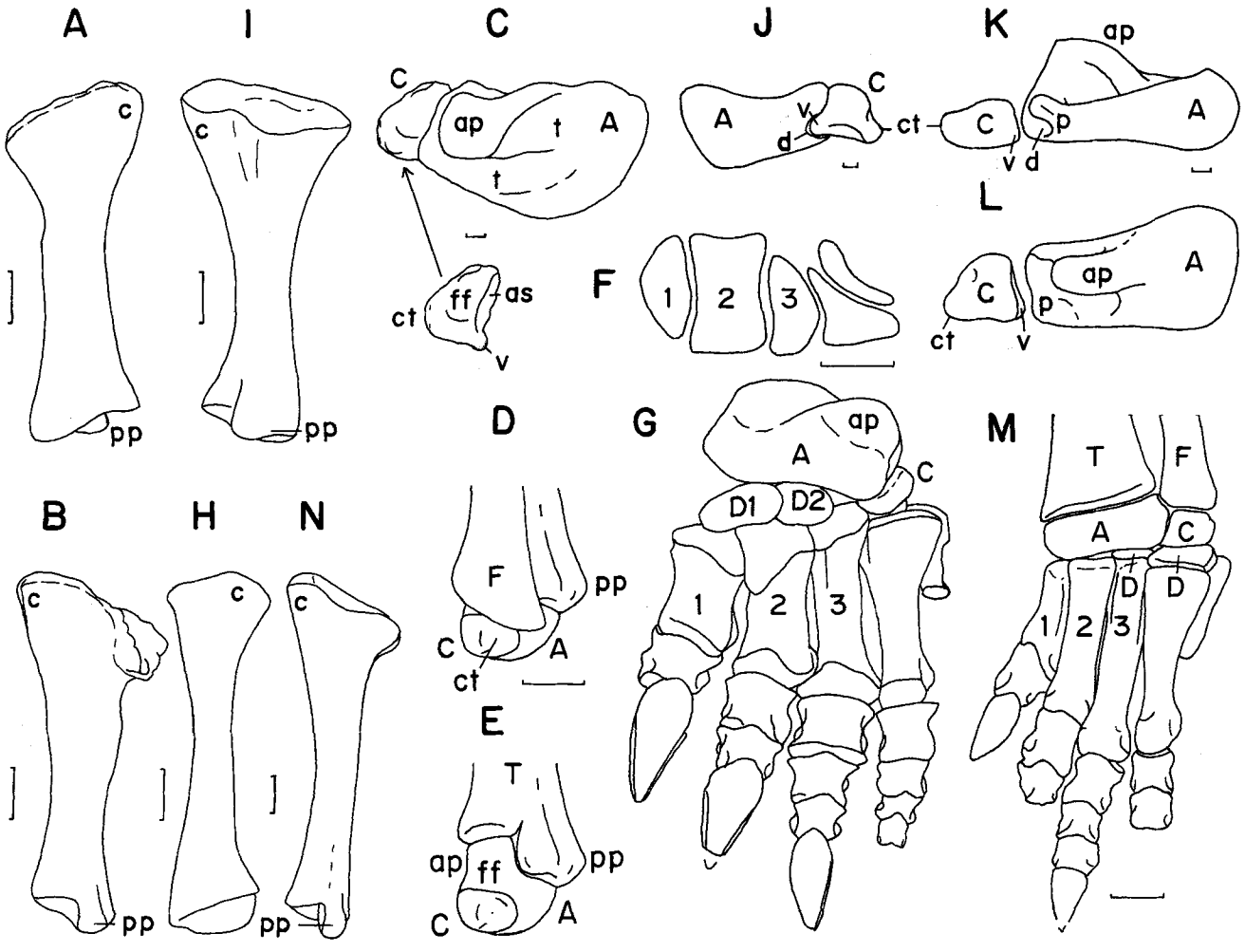


Fig. 1. A-G: *Blikanasaurus cromptoni* GALTON & VAN HEERDEN, holotype specimen SAM K403, a partial left hindlimb. - **A-B:** Tibia (A: anterior and B: lateral views). **C:** Astragalus and calcaneum in proximal (dorsal) view, articulated and with calcaneum alone (cf. Fig. 4B, F). **D-E:** Distal end of tibia in lateral view with astragalus and calcaneum with D: Fibula in articulation and E: Fibula removed (cf. Fig. 5D). **F:** Metatarsals in proximal view, after A. W. CROMPTON in RAATH (1972). **G:** Proximal and distal tarsals plus pes in anterior view (cf. Fig. 5E) (ungual phalanx of digit III lost or mislaid, outline from CROMPTON & WAPENAAR, unpublished MS). - **H-M:** Melanorosaurid *Riojasaurus incertus* from Los Colorados Formation of La Rioja, Argentina, bones of left hindlimb. **H-I:** Tibia (PVL 3808, after BONAPARTE 1972) (H: anterior and I: lateral views). **J:** Astragalus and calcaneum (PVL 3835, after NOVAS 1989) in distal (ventral) view. **K-L:** Astragalus and calcaneum (PVL 4364, after NOVAS 1989, reversed) (K: posterior and L: proximal (dorsal) views). **M:** Distal end of tibia and fibula plus tarsals and pes in anterior view, PVL 3536, after BONAPARTE (1972). - **N:** Plateosaurid *Euskelosaurus browni*, SAM 3341, left tibia in lateral view (after VAN HEERDEN 1979, reversed). – Scale bars equal 5 cm (A, B, F-I, M, N) and 1 cm (C-E, J-L).

surface of the astragalus is rounded (Fig. 4D), thus forming a 'rolling joint' with the two distal tarsals. The lateral surface of the astragalus has a shallow depression medioventrally (Fig. 4A, C, D) for the calcaneum (Figs. 1C, D, G, 3B, 5D, E). As in melanorosaurids, the ventromedial projection of the calcaneum fits into this depression (Figs. 1C, E, J-L, 3B, 5D), with the distal end of the fibula making contact with the astragalus just above it (Fig. 1D, M). In *Blikanasaurus* the calcaneum is relatively smaller so its contact with the astragalus is also more restricted; furthermore, it articulates with the flat, ventrolateral surface of the latter element.

Calcaneum (Figs. 1C-E, G, 3B, 4E-H, 5D, E)

CROMPTON & WAPENAAR (unpublished, quoted by EWER 1965: 434) believed the calcaneum to be absent, but described three distal tarsals. However, when the relationships between the tibia, fibula, astragalus and calcaneum of *Blikanasaurus* (Figs. 1C-E, G, 3B, 5D, E) are compared to those of *Riojasaurus* (Fig. 1J-M), it is apparent that the supposed third distal tarsal is the calcaneum that is a small nubbin of bone. Its medial surface (Fig. 4G) is triangular in outline and flat, to fit the corresponding surface of the lateroventral depression of the astragalus. The ventromedial projection of the calcaneum

(v, Figs. 1C, 4E, F) that fitted into this depression is intermediate in size between two specimens of *Riojasaurus* (Fig. 1J-L). However, the remnant of the calcaneal tuber (ct, Figs. 1C, J-L, 3B, 4F, H, 5D) is less prominent than it is in either specimen of *Riojasaurus*. The fibula rested on the dorsal surface of the calcaneum (Figs. 1D, 4F), while the convex ventral surface (Fig. 4E) contacted the fourth metatarsal (Figs. 1G, 5E).

Distal tarsals (Figs. 1G, 4I-L, 5E)

There are only two distal tarsals that are called the first and second as a matter of convenience. The first is subcircular and the second more elliptical in outline (Fig. 4J, L). Both are flattened discs with rounded edges (Fig. 4I, K). In reconstructing the tarsus all possible positions of these two, which have a natural fit on one another, were tried, but the most natural position is that shown (Figs. 1G, 5E). If the distal tarsals are placed in a lateral position as in *Riojasaurus* (Fig. 1M), then they only interpose between the astragalus and the third and fourth metatarsals. In this position the massive, and presumably weight-bearing, second metatarsal would then have been separated by cartilage from the astragalus. However, metatarsal V would articulate with distal tarsal II as in other prosauropods. As figured, in a more medial position, the weight would be transmitted from the tibia to metatarsals I to II via the astragalus and the distal tarsals, but the distal tarsals could well have been in a more lateral position as in *Riojasaurus*.

Metatarsals (Figs. 1F, G, 5E)

As is the case with the epipodials, the metatarsals are remarkably stocky compared to those of other prosauropods.

Metatarsal I (Figs. 1F, G, 3A, 5E, 6A-D). – Metatarsal I has a proximal surface which is a parallelogram with the minimum thickness (measured more of less anteroposteriorly) being 34 mm while the long sides are each ±50 mm long. The proximomedial surface is inclined posteriorly. The posterolateral surface has a low, rounded projection that fits into a shallow concavity in the proximomedial face of the second metatarsal. The distal articulation is divided into two unequal condyles, the lateral one being larger so that the first digit must have pointed slightly medially.

Metatarsal II (Figs. 1F, G, 5E, 6I-L). – This is the most massive metatarsal and it is illustrated with metatarsal III to which it is still affixed (Fig. 6I-L). The proximal surface of the second metatarsal has an hour-glass shape, the anterior and posterior edges being more or less straight (Fig. 1F). Each of these two (short) sides measures approximately 54 mm while the minimum transverse measurement of the proximal surface is 37 mm. The distal articulation is divided into two unequal condyles, the lateral one being larger; however, the size difference is not as obvious as in the first metatarsal.

Fig. 2. *Blikanasaurus cromptoni*, SAM K403. – **A-M:** Phalanges of left pes, in anterior (dorsal) (A, B, E, G, H-K, M), lateral (C, L) and posterior (ventral) (F) views. **A-C:** First digit (A: Phalanx 1; B, C: Ungual phalanx); **D-G:** Second digit (D: Phalanx 1; E, F: Phalanx 2; G: Ungual phalanx); **H-J:** Third digit (H: Phalanx 1; I: Phalanx 2; J: Phalanx 3); **K-M:** Fourth digit (K, L: Phalanges 1-3; M: Phalanx 4). – **N-Q:** Left tibia, in N: lateral (see Fig. 1B), O: posterior, P: anteromedial (cf. Fig. 1A) and Q: medial (& slightly posterior) views. – Scale bars equal 1 cm (A-M) and 5 cm (N-Q).

Metatarsal III (Figs. 1F, G, 5E, 6I-L). – The proximomedial side of metatarsal III is shaped to fit the concave proximolateral surface metatarsal II (Fig. 1F). Proximolaterally there is a rounded ridge that fits into a groove on the proximomedial face of metatarsal IV (Fig. 1F). The distal end is divided into two condyles, the medial one being the larger.

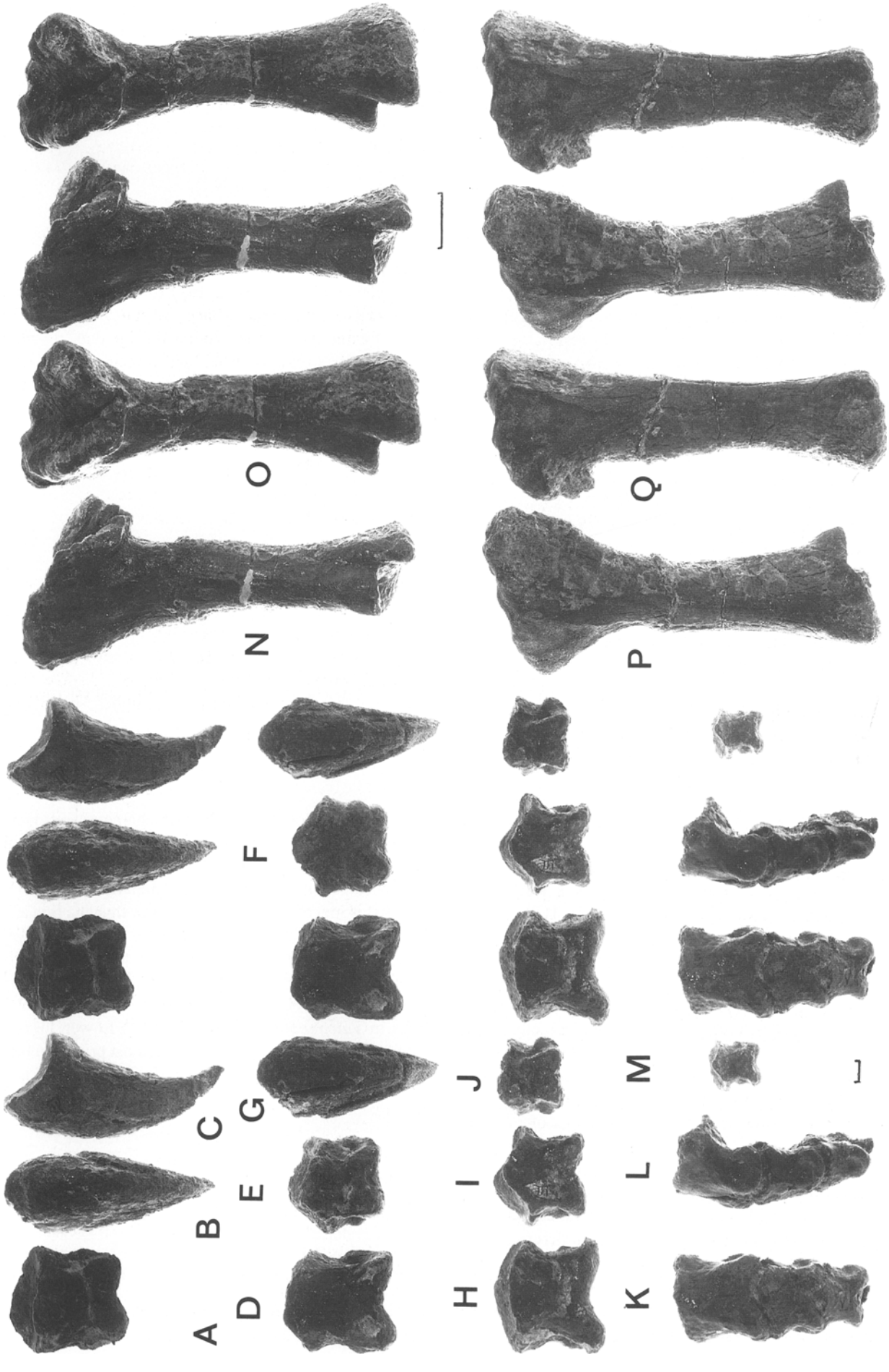
Metatarsal IV (Figs. 1F, G, 5E, 6E-H). – Metatarsal IV is appreciably less robust than the first three metatarsals which correlates with the reconstruction of the tarsus as described above. The proximal surface is roughly triangular in outline with the short base anteriorly and the longest side posterolaterally (Fig. 1F). Whereas the sides of the shafts in II and III are more or less parallel to one another in anterior view, those of IV are not. The medial margin forms a more or less straight line, but the lateral margin forms a long curve from the expanded proximal end to the constricted distal end (Fig. 6E, G). The distal end is not clearly divided into two condyles (Fig. 6E, G).

Metatarsal V (Figs. 1F, G, 4M-P, 5E). – Metatarsal V is much reduced compared even to the first. The minimum thickness of the proximal end is 15 mm. The proximal half of the medial surface is flat (Fig. 4M) to fit the similarly flat proximolateral surface of metatarsal V (Fig. 1F). In anterior (dorsal) view the fifth metatarsal is almost completely obscured by the fourth (Figs. 1G, 5E). The lateral surface is concave in the proximal half (Fig. 4O). The distal half of the element is rounded and tapers to a tip. The articular surface at the distal end is slightly damaged, but the surface must have been comparatively small and, if there was a phalanx, then it must also have been very small as in *Yunnanosaurus* (GALTON 1992).

Phalanges (Figs. 1G, 2A-M, 3A, 5E)

The ungual phalanx of the third digit has been lost or mislaid (Figs. 1G cf. 5E) and one or two phalanges are missing (i.e. the ungual of the fourth digit, possibly a small phalanx from the fifth digit). The phalanges are similar in shape to those of other early saurischians. It is noteworthy that the phalanges are not nearly as stockily-built as the tibia and metatarsals I to III, their proportions being more comparable to those of the plateosaurid *Plateosaurus* (GALTON 1992; VON HUENE 1932).

Relationships: In terms of the ankle region, CHARIG et al. (1965) characterized the Sauropodomorpha as hav-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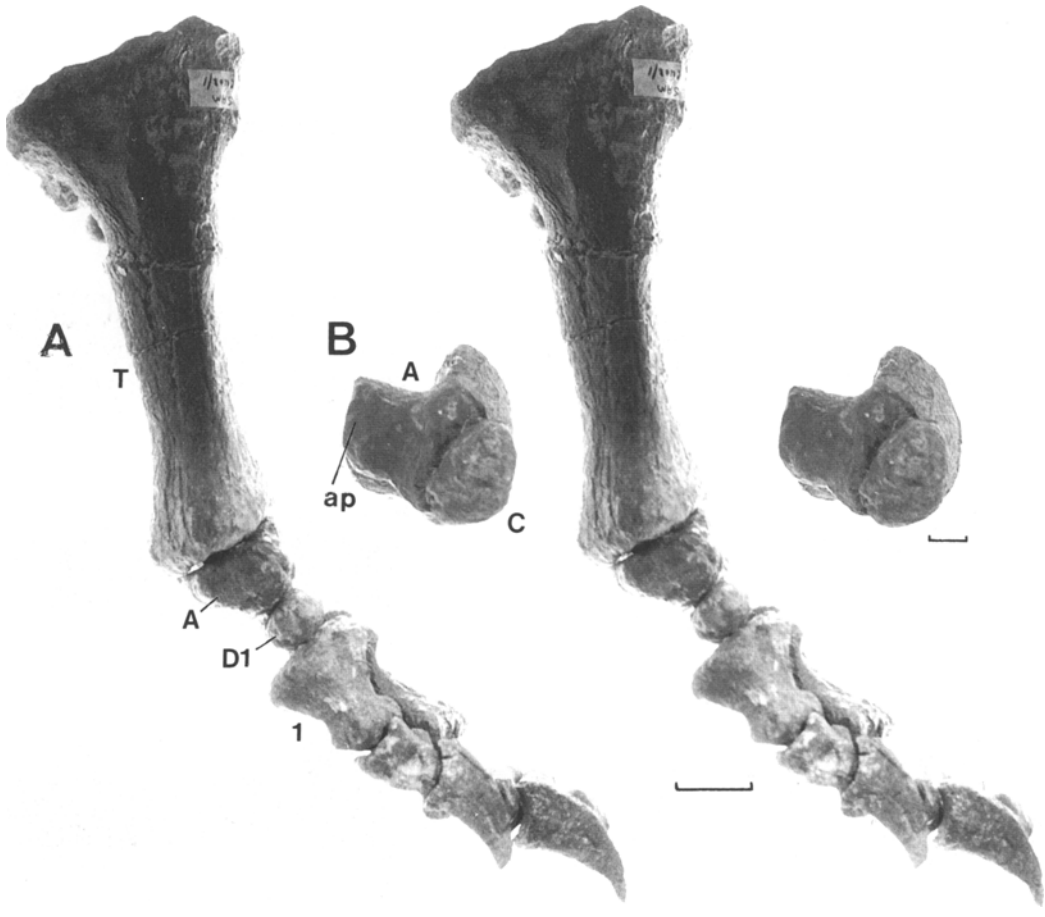
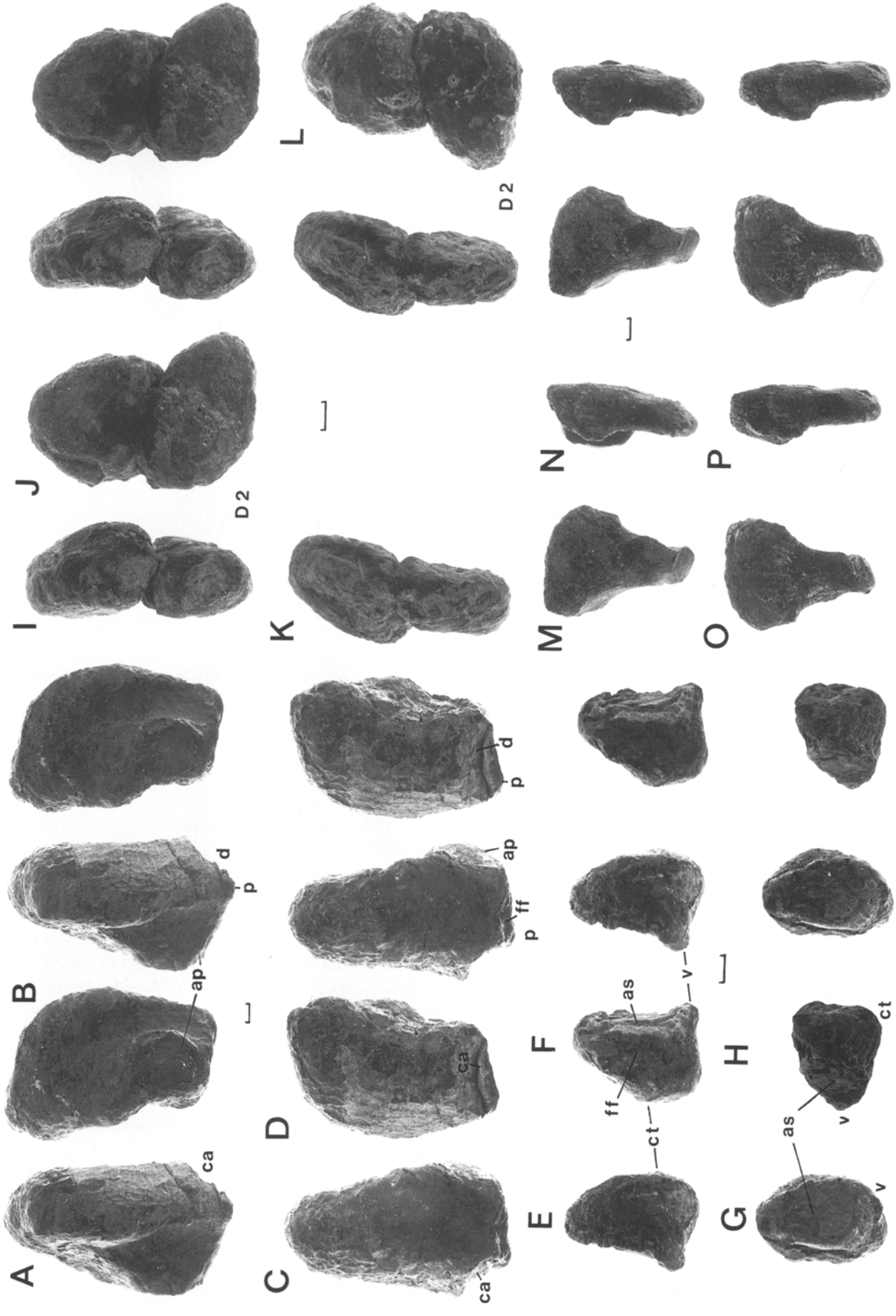


Fig. 3. *Blikanasaurus cromptoni*, SAM K403. - **A:** Left partial hindlimb in medial view; **B:** Left astragalus and calcaneum in lateral view (cf. Figs. 1E, 5D). – Scale bars equal 5 cm (A) and 1 cm (B).

ing the connection between the crus and tarsus strengthened by a posterior descending flange on the back of the tibia and a central ascending process on the astragalus. On this basis, *Blikanasaurus* is clearly a sauropodomorph, and the form of this region (Figs. 1C-E, 4A-H, 5D, E) is more similar to that of prosauropods than to that of sauropods (CHARIG et al. 1965). In the pes, sauropods are characterized by having a long metatarsal V (CRUICKSHANK 1975). The condition in *Blinkanasaurus* with a vestigial metatarsal V (Figs. 1G, 5E), closely resembles that of prosauropods (Fig. 1M; GALTON 1992). Consequently, *Blikanasaurus* is referred to the Prosauropoda.

The tibia, and especially the metatarsals, of *Blikanasaurus* (Fig. 1A, B, G) are much more robust than those of other prosauropods (GALTON 1992), including melanorosaurids (Fig. 1H, I, M, N). Metatarsals II and III (Figs. 1G, 5E, 6I-L) are uniquely massive, especially in side view (Fig. 6J, K). Because of these differences from other prosauropods, including melanorosaurids, the family Blikanasauridae was erected for *Blikanasaurus* by GALTON & VAN HEERDEN (1985). CHARIG et al. (1965) briefly discussed the affinities of *Blikanasaurus* and concluded that, although it has certain characteristics reminiscent of the Sauropoda, it cannot be regarded as an ancestral form for this group. There can be no doubt that *Blikanasaurus* has a reduced fifth metatarsal (Figs. 1G, 5E), that is much less robust and shorter than the first and, for this reason, it was excluded by GALTON & VAN HEERDEN (1985) from the evolutionary line leading to the Sauropoda that are characterized by having an unreduced fifth metatarsal (CRUICKSHANK 1975). Metatarsal V is large in *Vulcanodon* (COOPER 1984), a Lower Jurassic member of the Vulcanodontidae, the most primitive family of the Sauropoda (MCINTOSH 1992). However, as J.

Fig. 4. *Blikanasaurus cromptoni*, SAM K403. - **A-D:** Left astragalus, in A: posterior, B: dorsal or proximal (cf. Fig. 1C), C: anterior, D: ventral or distal views. **E-H:** Left calcaneum, in E: ventral, F: dorsal or proximal (cf. Fig. 1C), G: medial and H: anterior views. **I-L**: Left distal tarsals 1 and 2, in I: anterior, J: ventral or distal, K: posterior and L: dorsal or proximal views. **M-P:** Left metatarsal V, in M: anterior, N: lateral (and slightly ventral), O: posterior and P: lateral (and slightly dorsal) views. – Scale bars equal 1 cm.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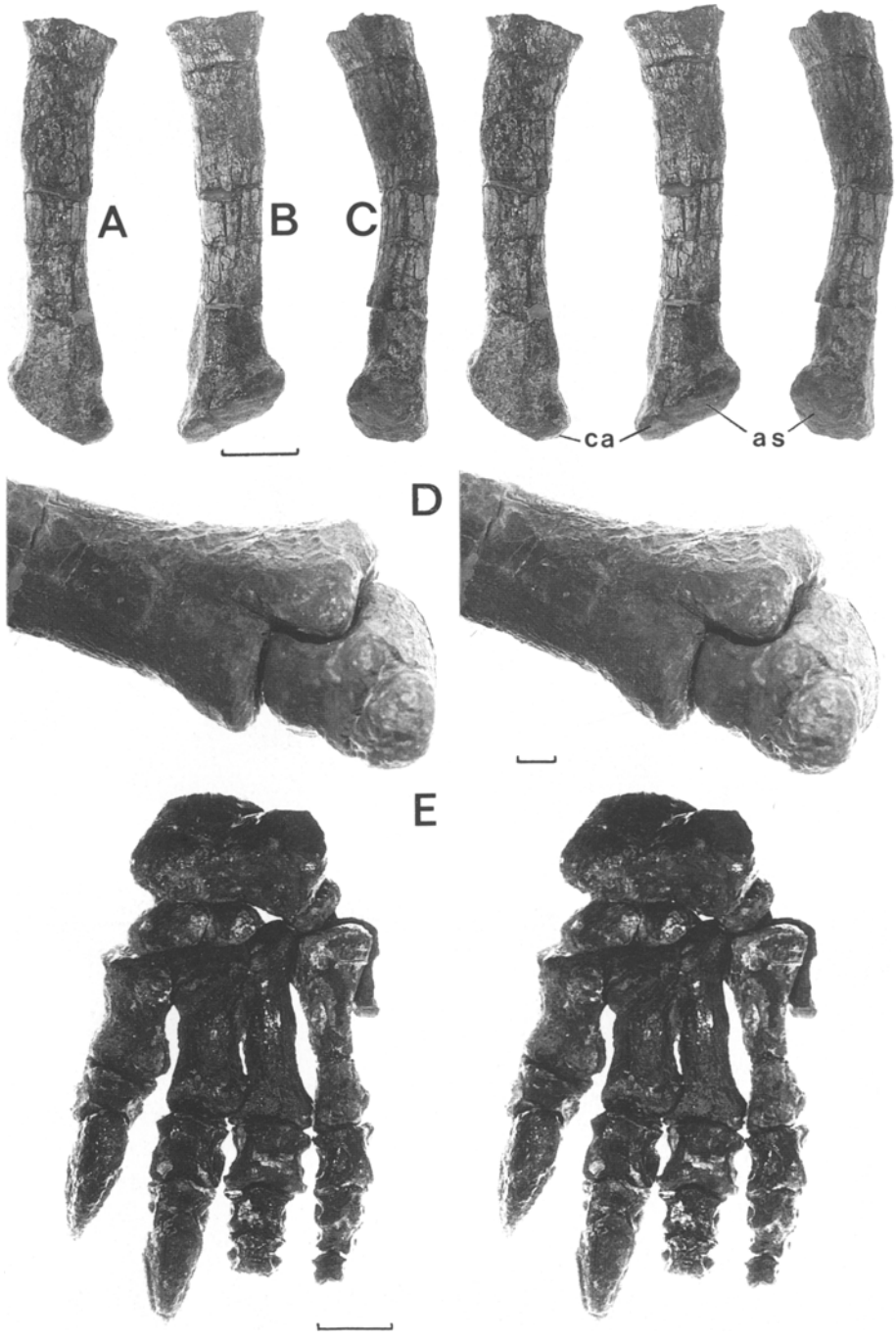


Fig. 5. *Blikanasaurus cromptoni*, SAM K403. - **A-C:** Left fibula (lacking proximal part) in A: lateral, B: medial and C: anterior views. **D:** Distal end of left tibia, astragalus and calcaneum in lateral view (cf. Figs. 1E, 2B). **E:** Left proximal tarsals and pes in anterior view (cf. Fig. 1G). – Scale bars equal 5 cm (A-C, E) and 1 cm (D).

BONAPARTE (pers. comm.) notes, we do not know anything about the ontogeny of metatarsal V in *Blikanasaurus*, or in sauropods, and it is possible that heterochronic processes were involved during the development of metatarsal V in the line leading to sauropods. However, on the basis of the morphology of the hindlimb in the adult, it is concluded that, although *Blikanasaurus* was an early quadrupedal saurischian, it was not the ancestor for the Sauropoda.

The earliest record of the Prosauropoda

WALKER (1969: 473) noted that a tooth and a cervical vertebra, from the Bromsgrove Sandstone Formation (Middle Triassic, Anisian/Ladinian, see BENTON et al. 1994) of the central Midlands of England, appear to represent a primitive prosauropod dinosaur. These specimens, that are listed as "prosauropod" by BENTON et al. (1994: 140), predate the earliest record of Carnian (Up-

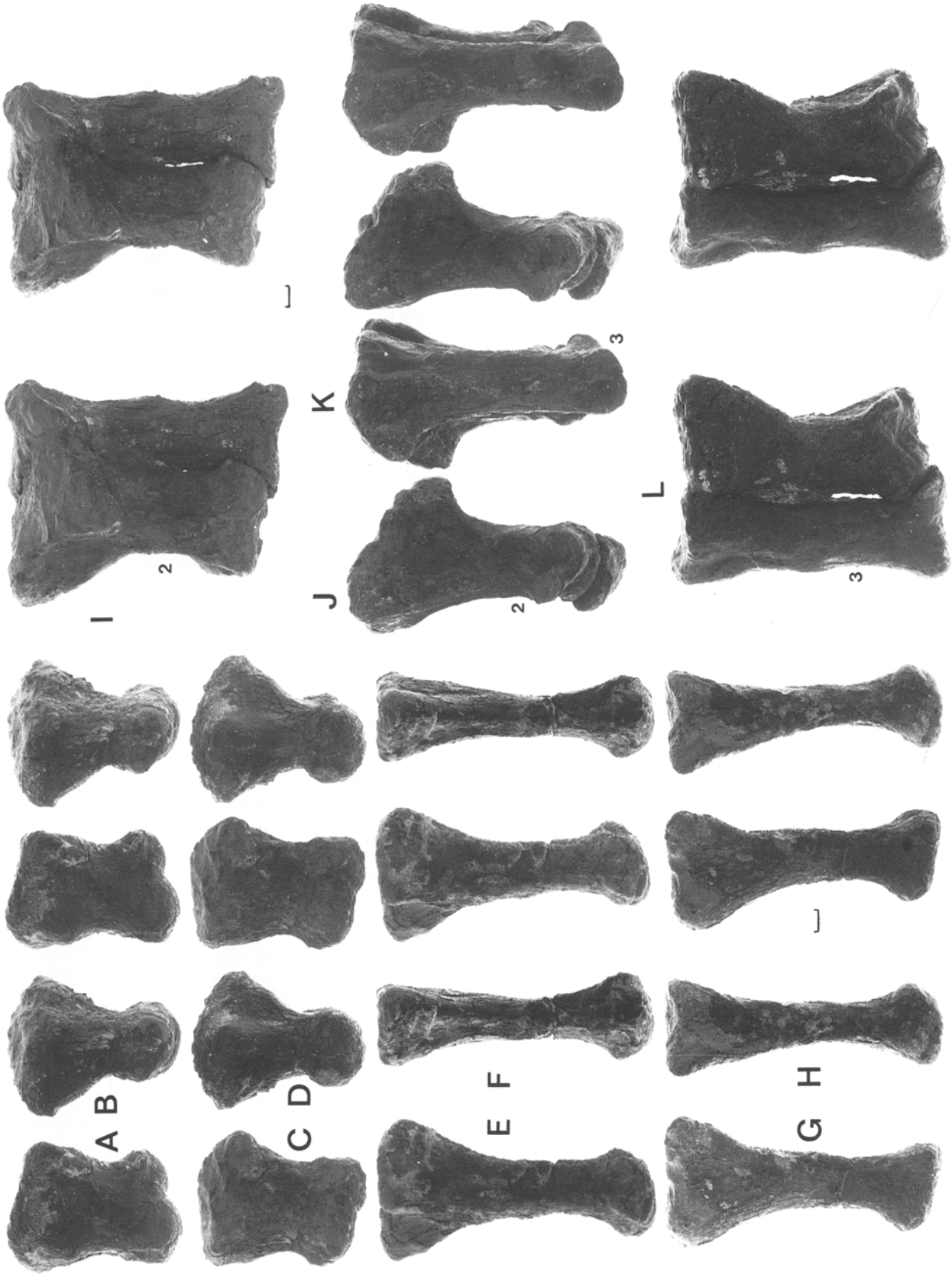


Fig. 6. *Blikanasaurus cromptoni*, SAM K403. - **A-D:** Left metatarsal I, in A: posterior, B: medial, C: anterior and D: lateral views. **E-H:** Left metatarsal IV, in E: anterior, F: lateral, G: posterior and H: medial views. **I-L:** Left metatarsals II and III, in I: anterior, J: medial, K: lateral and L: posterior views. – Scale bars equal 1 cm.

per Triassic) given by BENTON (1993) for the Prosauropoda. However, these specimens are not prosauropod (GALTON & WALKER 1996). The tooth of "*Thecodontosaurus*" (GALTON 1985b: fig. 3A; GALTON & WALKER 1996: fig. 2C) is probably from a phytosaurid thecodontian (Parasuchia). The partial posterior cervical vertebra is similar to one of *Melanorosaurus* (VAN HEERDEN & GALTON 1997: fig. 1B) but, on the basis of synapomorphic characters, it can be diagnosed only as that of a Dinosauriformes (*Marasuchus* plus Dinosauria). BENTON (1993) lists the thecodontosaurid *Azendohsaurus laaroussi* DUTUIT 1972, represented by jaws and teeth from the Argana Formation (Carnian, Upper Triassic) of Marrakech, Morocco (see GAUFFRE 1993b), as the earliest record of the Prosauropoda.

Although not specifically discussed in the text or listed by SHUBIN & SUES (1991: Appendix I), the lower Elliot Formation of South Africa has a faunal assemblage of traversodontid cynodonts and rauisuchid thecodontians that they consider to be typical of a Carnian age. This omission was rectified by GAUFRRE (1993a), who concludes that the age of the lower Elliot Formation is Carnian, possibly even early Carnian, rather than Carnian/Norian (GALTON 1992) or Norian (BENTON 1993). Consequently, the fauna of the lower Elliot Formation of South Africa includes the oldest record for articulated remains of the Prosauropoda and the first evidence for the radiation of the group, with three families represented, the plateosaurid *Euskelosaurus* (see VAN HEERDEN 1979), the melanorosaurid *Melanorosaurus* (see VAN HEERDEN 1979; VAN HEERDEN & GALTON 1997) and the blikanasaurid *Blikanasaurus*. These genera are the earliest record for their respective families, and probably also for the Prosauropoda as a group. It should be noted that BENTON (1993) incorrectly included *Euskelosaurus* with *Melanorosaurus* as the earliest record of the Melanorosauridae rather than of the Plateosauridae.

Notes on the fauna of the lower Elliot Formation

The sedimentology of the Stormberg Group of southern Africa is reviewed by VISSER (1984). The fauna of the lower Elliot Formation (Lower Red Beds of Stormberg Series, = 'Passage Beds', 'Upper Molteno') is discussed by OLSEN & GALTON (1984, as Lower Stormberg assemblage), KITCHING & RAATH (1984, as *Euskelosaurus* Range Zone) and HOPSON (1984). It is important because it is the earliest terrestrial fauna (Carnian, Upper Triassic), with a radiation of herbivorous archosaurs (prosauropods), that preceeded the later, better known Norian faunas of the uppermost Triassic (see SHUBIN & SUES 1991 for details).

Amphibia

Amphibians are represented by a stereospondyl, probably a capitosaurid, and the undescribed remains include parts of skulls and jaws (listed by KITCHING & RAATH 1984).

Thecodontia – Rauisuchia

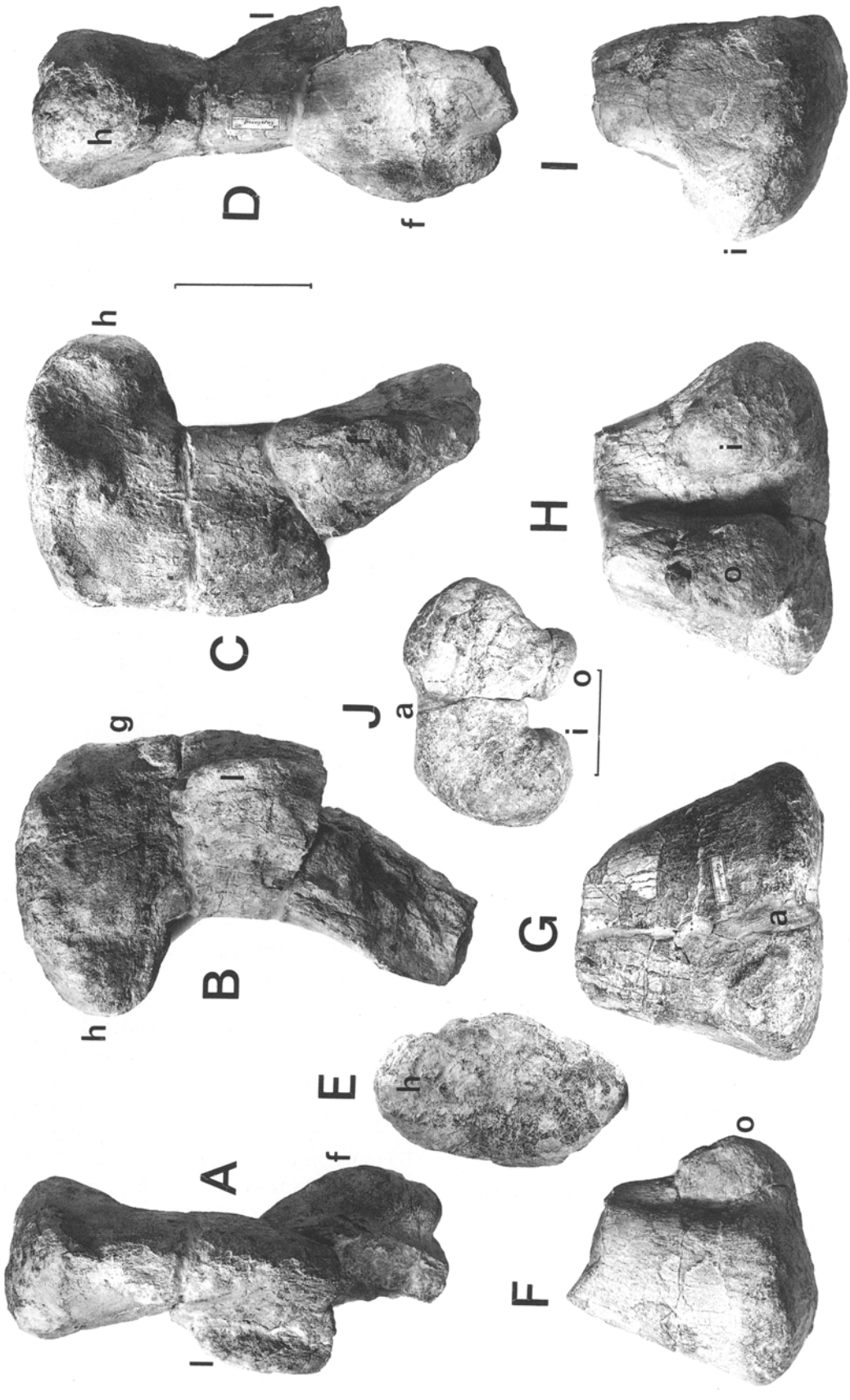
Large serrated teeth of carnivorous forms are found in the lower Elliot Formation and were named *Bastudon ferox* VON HUENE 1932. Isolated teeth of this type are often found in association with large prosauropod bones. This association was noted by VON HUENE (1932; see CHARIG et al. 1965 for additional references), and it led COOPER (1980) to argue that the large early prosauropods were carnivorous. KITCHING & RAATH (1984) described (but did not figure) a maxillary fragment with similar teeth in situ (and with similar isolated worn teeth) that was associated with large postcranial elements and osteoderms. This find was tentatively regarded as representing a rauisuchid thecodontian. This identification is strengthened by the presence of osteoderms, a character that is well developed in rauisuchids but extremely rare in carnivorous theropod dinosaurs. Another possible rauisuchid maxilla with teeth is mentioned by HOPSON (1984) and several possible rauisuchid specimens are listed by KITCHING & RAATH (1984). However, to date none of this rauisuchid material has been illustrated or properly described. Most of the ichnotaxa described by ELLENBERGER (1970) are referred to *Brachychirotherium* spp. by OLSEN & GALTON (1984) and these were probably made by a thecodontian reptile, ? rauisuchid (OLSEN & GALTON 1984).

Dinosauria incertae sedis

The holotype of *Aliwalia rex* GALTON, 1985c is a large femur lacking the shaft (Fig. 7; calculated maximum length of bone 900-1000 mm) in Vienna that, although there is no locality data with the specimen, probably came from the same excavation site as the lectotype of *Euskelosaurus brownii* HUXLEY 1866 (i.e. Barnard's Spruit about 24 km south of Aliwal North, see discussion under Plateosauridae).

The femur (Fig. 7; casts at GPIT) was originally described by VON HUENE (1906: 131-132, figs. 41, 42; pl. 16, fig. 2; pl. 17, fig. 1) as ?*Euskelosaurus* and it was included as part of the paralectotype of *Euskelosaurus browni* HUXLEY 1866 by COOPER (1980: 13, fig. 8), but this is incorrect. This femur differs from those of *Euskelosaurus* and other plateosaurids (see GALTON 1985a; 1992; VAN HEERDEN 1979) in that the head is medially directed and it is separated by a relatively narrow neck from the shaft (Fig. 7A, D); the lesser trochanter is repre-

Fig. 7. Dinosauria incertae sedis *Aliwalia rex* GALTON 1985c. Holotype. Incomplete left femur from lower Elliot Formation (Upper Triassic) of South Africa, probably from Barnard's Spruit near Aliwal North. - **A-E:** Proximal end NMW 1889-XV-39 in A: lateral, B: anterior, C: posterior, D: medial and E: proximal views. **F-J:** Distal end NMW 1876-VII-B124 in F: lateral, G: anterior, H: posterior, I: medial and J: distal views. – Scale bars equal 10 cm (note that A-D, F-I reduced less than E, J).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sented by a 100 mm long crest that does not terminate in a point (Fig. 7A, B, D); the distal end of the pendant fourth trochanter (Fig. 7A, D) is 340 mm from the proximal end of the femur so it is very proximally placed; and the form of the distal condyles (Fig. 7F-J) differs from those of *Euskelosaurus*. The proximal end (Fig. 7E) measures 215 x 120 mm, the minimum distance from the head to the distal edge of the fourth trochanter (Fig. 7D) is 336 mm, and distally (Fig. 7J) the maximum width and maximum anteroposterior widths across the inner and outer condyles are 261, 165 and 187 mm, respectively.

GALTON (1985c) concluded that *Aliwalia* was more closely related to *Herrerasaurus* and *Staurikosaurus* from the Upper Triassic of South America than it was to Triassic coelurosaurs and Jurassic carnosaurs. He referred *Aliwalia* to the Herrerasauria but SUES (1992) regarded it as Dinosauria incertae sedis. The latter referral is followed because the femur of *Aliwalia* differs in several respects from that of *Herrerasaurus* as described by NOVAS (1993). In particular, the femur of *Aliwalia* lacks a prominent trochanteric shelf passing posteriorly from the lesser trochanter that is much larger than that of *Herrerasaurus*.

SEELEY (1894: 318-320, fig.1) described a large (about 420 mm long, certainly "more than 40 mm [sic] long" as noted by GALTON 1985c: 16) left premaxilla and maxilla (BMNH R3301, Fig. 8A) with replacement teeth in situ that came from the lower Elliot Formation of Barnard's Spruit about 24 km south of Aliwal North. This was probably the same excavation site as that of the lectotype femur of *Euskelosaurus browni* and the holotype femur of *Aliwalia rex* (see discussion under Plateosauridae). The bones are exposed in medial view but, apart from the dorsal process, most of the bone was removed by weathering to expose fourteen alveoli, twelve of which are in the maxilla. Three replacement teeth are preserved in the dental alveoli (Fig. 8A). The largest tooth sits within the remnants of the root of the functional tooth and ten serrations are preserved on its posterior edge (Fig. 8B). CHARIG et al. (1965: 206-207) noted that the teeth (Fig. 8), that they did not figure, "are much broader and less pointed than those of a typical Jurassic carnosaur; they are very compressed labio-lingually with sharp crenulate anterior and posterior margins and one is slightly recurved, while the apex of the other appears to be directed straight downward. Altogether they give little indication of the animal's affinities." However, this specimen is definitely not referable to *Euskelosaurus* which is a prosauropod in which this type of teeth do not occur (GALTON 1985b).

This maxilla with carnivorous teeth lacks any derived characters diagnostic of a rauisuchian thecodontian (BENTON 1986) or of an early carnivorous saurischian such as *Herrerasaurus* (SERENO & NOVAS 1992). However, it is of an appropriate size to go with the holotype femur of *Aliwalia rex* that probably came from the same excavation site (it could even be from the same animal), so the maxilla (Fig. 8) is tentatively referred to *Aliwalia*.

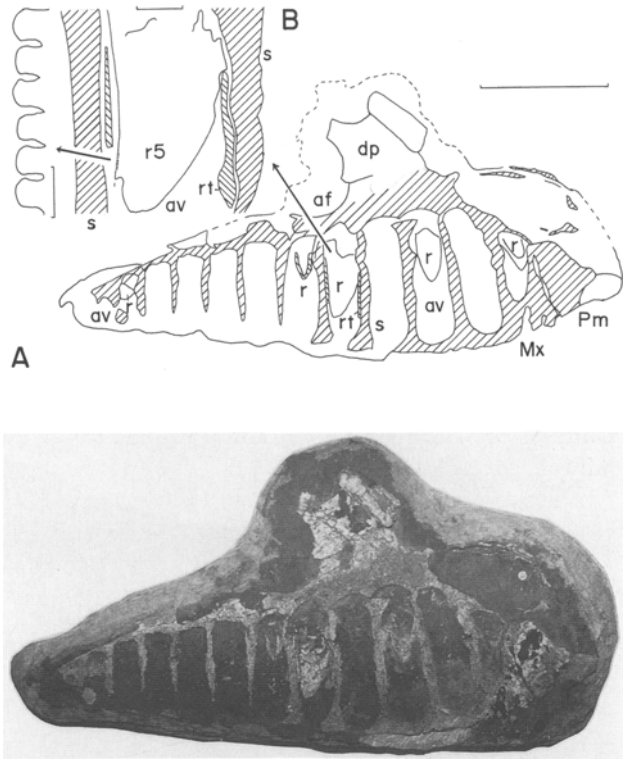

Fig. 8. Dinosauria incertae sedis *Aliwalia rex*, referred specimen BMNH R3301 from lower Elliot Formation of Barnard's Spruit near Aliwal North. - **A:** Left maxilla and premaxilla in medial view, photograph and explanatory outline. **B:** Replacement tooth in alveolus 5, with detail of posterior serrations. Broken bone indicated by mechanical shading. – Scale bars equal 10 cm (A), 1 cm (B, tooth) and 1 mm (B, tooth serrations).

It should be noted that the partial lower jaw and a cervical vertebra from the Kraai River, to the south-east of Aliwal North, that were collected and described as *Euskelosaurus browni* by SEELEY (1894: 335-340, figs. 6, 7), were referred to the early Triassic thecodontian *Erythrosuchus africanus* by BROOM (1911: 292) and VON HUENE (1911, following letter from BROOM).

Theropoda

Theropod dinosaurs are represented by several of the ichnotaxa of ELLENBERGER (1970) that were referred to *Grallator* spp. by OLSEN & GALTON (1984).

Sauropodomorpha – Prosauropoda

Plateosauridae

The common prosauropod dinosaur from the lower Elliot Formation is *Euskelosaurus browni* HUXLEY 1866. SEELEY (1894: 318) noted that ALFRED BROWN sent four separate collections "of the same animal" of *Euskelosaurus browni* to Europe, and that these were described by HUXLEY (1866, first London shipment), FISCHER (1879, Paris shipment) and SEELEY (1894, third London

shipment). SEELEY (1894) was unable to locate the second London shipment and COOPER (1980; cited by GALTON 1985c) suggested that it may be represented by the material in Vienna. However, this is not so because BROOM (1911: 292) mentions the lost London shipment plus "a still later shipment (that) was sent to Vienna." BROOM (1911: 292) did note that "Mr. BROWN informs me that all these collections were got at the same spot." However, two different locations have been given for this spot. HUXLEY (1866: 4), who quoted from a letter from Mr. BROWN, noted that the fossils were obtained "in the division of Aliwal North and about thirty miles from the town of Aliwal North." SEELEY (1894: 317) gave the locality as "Barnard's Spruit, Ward, 15 miles south of Aliwal North." HAUGHTON (1924: 424) noted that *Euskelosaurus browni* HUXLEY 1866 was "almost certainly from the Kraai River." KITCHING & RAATH (1994: 118) list both localities for *E. browni* HUXLEY 1864, viz. "Aliwal North - Kraai River - (?) 3027DB/3027CD" and "Albert (Burgersdorp) - Barnard's Spruit (Ezelsklip) - (?) 3026DC Kramberg (?) 30° 57'S 27° 37'E." However, COOPER (1980: 12) quoted SEELEY (1894: 335) that he visited a locality with Mr. BROWN on the "Kraai River, to the south-east of Aliwal North, which we anticipated might furnish Euskelosaurian remains." As COOPER (1980) noted, this wording suggests that *Euskelosaurus* had not been previously detected along the Kraai River, so this was not the type locality of *E. browni* and, as SEELEY most likely visited the type locality with BROWN, the lectotype locality of "Barnard's Spruit, Ward, 15 miles (about 24 km) south of Aliwal North" is more likely to be correct. The register entry for BMNH R2516, the lectotype of *Euskelosaurus browni,* notes that the material, donated by HUXLEY in 1888, came from South Africa; the most detailed information, on the label with BMNH R1625c (proximal end of left tibia and fibula), only gives the locality as Aliwal North. There is no locality information with the femur of *Aliwalia rex* (Fig. 7) but the register entry for the referred maxilla (BMNH R3301, Fig. 7), donated by Mr. BROWN in 1905, gives the locality as Barnard's Spruit, Ward, Cape Colony.

Euskelosaurus has long been referred to the Melanorosauridae (including COOPER 1980; BENTON 1993), but VAN HEERDEN (1979) showed that it is a large plateosaurid (total body length approximately 10 m). The synonymy of *Euskelosaurus* is discussed by VAN HEERDEN (1979) and summarized by KITCHING & RAATH (1984), who list numerous undescribed specimens of this prosauropod dinosaur. However, despite its commonness in the lower Elliot Formation as bones, the only footprints from this formation that are attributed to prosauropods are those of *Tetrasauropus unguiferus* ELLENBERGER 1970 (see OLSEN & GALTON 1984).

Melanorosauridae

The holotype (SAM 3450) of the prosauropod dinosaur *Melanorosaurus readi* HAUGHTON 1924 was redescribed by VAN HEERDEN (1979), who regarded it as a junior synonym of the sympatric *Euskelosaurus browni* HUXLEY 1866. This synonymy was followed by COOPER (1980) and KITCHING & RAATH (1984). The femur of *Euskelosaurus* (BMNH R1625; VAN HEERDEN 1979; GALTON 1985a) is typically plateosaurid in being sigmoidal in posterior view with the fourth trochanter well removed from the medial edge as in most other prosauropods. However, in SAM 3450 the femur is straight in posterior view with the fourth trochanter close to or on the medial margin as in *Riojasaurus* from the Upper Triassic of Argentina (BONAPARTE 1972). The straightness of the femur is not the result of distortion; so GALTON (1985a; 1992) followed the earlier conclusions of VAN HEERDEN (1977) in accepting the validity of *Melanorosaurus readi* HAUGHTON 1924 and of the family Melanorosauridae VON HUENE 1929. KITCHING & RAATH (1984) list the large prosauropod *Roccosaurus tetrasacralis* VAN HEERDEN (unpublished, 1977). This taxon is based on a partial skeleton described by VAN HEERDEN (1977) from the lower Elliot Formation of the Wodehouse District of the Cape Province that is described elsewhere as a referred specimen of *Melanorosaurus* (VAN HEERDEN & GALTON 1997).

Therapsida

The bones of therapsids are rare, being represented by jaws and teeth of the large herbivorous traversodont cynodont *Scalenodontoides macrodontes* CROMPTON & ELLENBERGER 1957 (see HOPSON 1984). The only evidence for the presence of large anomodont dicynodonts, the dominant herbivorous therapsids of the Permian and Lower Triassic, are the footprints of *Pentasauropus maphutsengi* ELLENBERGER 1970 (OLSEN & GALTON 1984).

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